

THE DISTRIBUTION OF THE POLYCHAETE NEANTHES LIGHTI IN THE SALINAS RIVER ESTUARY, CALIFORNIA, IN RELATION TO SALINITY, 1948-1952

RALPH I. SMITH

Department of Zoology, University of California, Berkeley 4, California

The estuarine nereids, with representatives widely distributed, offer excellent material for studies in comparative physiology and ecology. The present study is part of an attempt to work out the nature of the adaptation to brackish waters as seen in one species occupying ecologically distinctive habitats within a limited geographical area. *Neanthes lighti* furnishes favorable material for studies of the invasion of fresh waters by marine annelids, since it equals or exceeds the much-studied *Nereis diversicolor* in its ability to live and reproduce in waters of low salinity. Its viviparous mode of reproduction, described in an earlier report (Smith, 1950), has perhaps been of adaptive significance in this respect. The fact that the species appears to consist of self-fertilizing hermaphroditic individuals, living in widely separated rivers, may have favored the appearance of local races, reproductively and spatially isolated from each other. In the Salinas River estuary, some twelve miles north of Monterey, California, the species occurs under a wide range of conditions, and so furnishes material for a study of ecological limitations and adaptations which can form a background for, and give meaning to, studies upon its physiology. As a preliminary to more detailed studies upon the mechanism of osmotic regulation, the present report describes the physical and biotic conditions under which *N. lighti* occurs in the Salinas River. These findings in themselves depict extremely variable estuarine conditions, and may be useful in studies on other animals, and in amplifying our information on estuaries in general. An understanding of the history of salinity changes in an estuary is a prerequisite for studies on the distribution and physiology of its inhabitants.

Observations were begun in 1948, coincidentally with other work, and have been carried out as opportunity offered until the fall of 1952. During certain periods the river could be visited only infrequently, hence the data include numerous gaps. However, the total four and one half year record does reveal in a general way the pattern of salinity changes in an estuarine system, and covers the full range of climatic conditions characteristic of this area. It is believed that the results clarify the relationship of salinity to climatic conditions, and will make future studies of estuaries in this area more rewarding.

PHYSICAL AND BIOTIC CONDITIONS IN THE SALINAS ESTUARY

The estuary of the Salinas River (Fig. 1) presents an extremely varied set of conditions, especially in relation to salinity. This variation in salinity characterizes estuaries in general; for an excellent discussion of estuarine conditions, the review by Day (1951) should be consulted. The Salinas falls into Day's category

of "blind" estuaries,¹ that is to say, it carries in most parts of the year so small a flow that across its mouth the sea builds up a barrier sand bar, blocking normal outflow and tidal exchange. When this has occurred, the estuary gradually freshens, often standing at a high level. In winter, flood conditions may occur

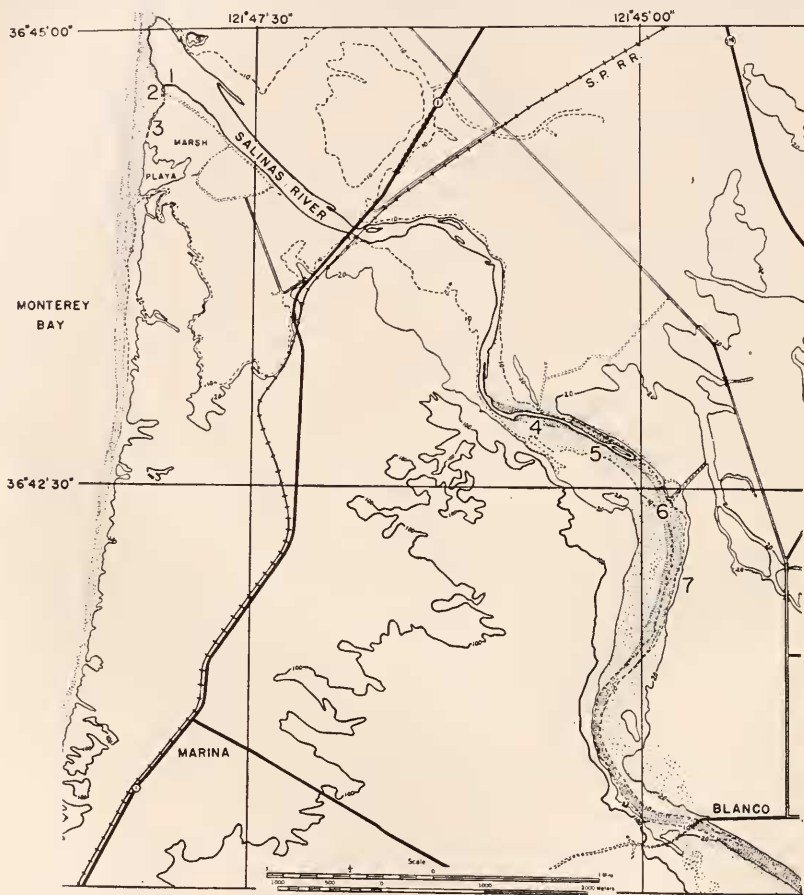


FIGURE 1. The estuary of the Salinas River, from Army Map Service sheets (Marina and Salinas quadrangles) compiled in 1947, to show locations 1-7 mentioned in text. Most of detail omitted; only 10, 20 and 100 foot contours shown.

following periods of heavy rain. In most years these seasonal freshets have caused the river to cut through the bar across its mouth, occasionally in the past rather violently, and with loss of life (MacGinitie, 1935), providing for a time an outlet to the sea. In recent years it has been the practice to excavate a channel through the barrier of sand in order to release the swollen river before flooding of farmlands oc-

¹ Judging from the account given by Scott, Harrison and Macnae (1952), the Klein River Estuary in South Africa bears a close general resemblance to the Salinas Estuary.

curs. With the breaching of the barrier, the lower and middle reaches of the estuary receive tidal influxes of sea water until the bar is reestablished. Thus the lower reaches for most of the year experience low salinity but are seasonally subjected to extreme fluctuations in salinity and exposure. The upper reaches of the estuary and marshes adjacent to the lower reaches also undergo salinity fluctuations, but not nearly so drastic in magnitude and rate of change. Were seasonal rainfall and the consequent fresh water discharge into the estuary uniform from year to year, a description of salinity conditions would be relatively simple, but in fact no such uniformity exists. In order to provide a background for understanding the changes in the river during the years 1948-52 of this study, rainfall and runoff records since 1944 have been compiled from published records (U. S. Depts. of the Interior and of Commerce). As shown in Figure 2, practically all of the rainfall in this region falls between September and April, and even within this span of months may be extremely concentrated, sending great freshets down into the estuary in certain winter months. The watershed of the Salinas is stated to be 4231 square miles, and rainfall varies considerably in different parts of the area. In order to make a rough estimate of the rainfall, the monthly rainfalls in inches reported from all

TABLE I

Total runoff in "second-foot-days"² entering Salinas Estuary by water-years (Oct.-Sept.), and totaled average rainfall at stations recording on Salinas River watershed

Water-year	Rainfall (inches)	Runoff
1944-45	12.11	157,147
1945-46	12.41	66,692
1946-47	9.25	3,513
1947-48	11.24	1,645
1948-49	11.56	25,500
1949-50	12.35	14,874
1950-51	10.21	17,862
1951-52	20.53	336,957

stations on the watershed (4 to 8 stations in most months) were averaged, and the sum of the monthly rainfalls taken as an expression of total rainfall for each water year (October through the following September). These estimates showed a more than two-fold variation in annual rainfall, from about 10 inches in the dry years 1946-48, to 20 inches in the extremely wet 1951-52 season (Table I).

Discharge into the estuary has been taken from the records of the gauging station at Spreckels, a few miles upstream, near the city of Salinas. These values show a far more extreme variation than do rainfall records, the total yearly discharge varying from 1645 second-foot-days² (142,128,000 cu. ft.) in 1947-48 to 336,957 second-foot-days (29,113,084,800 cu. ft.) in 1951-52 (Table I and Fig. 2). Impoundments and irrigation diversions undoubtedly greatly reduced the discharge in the years of low rainfall, and may have contributed materially to the stability which characterized the estuary prior to 1949. Variation from month to month is also extreme, the record of 173,901 second-foot-days in the month of February, 1952 exceeding the combined discharge of the six preceding water-years.

² One "second-foot-day" is the amount of water flowing in one day past a point at a rate of one cubic foot per second. It equals 86,400 cubic feet or 1.983 acre-feet.

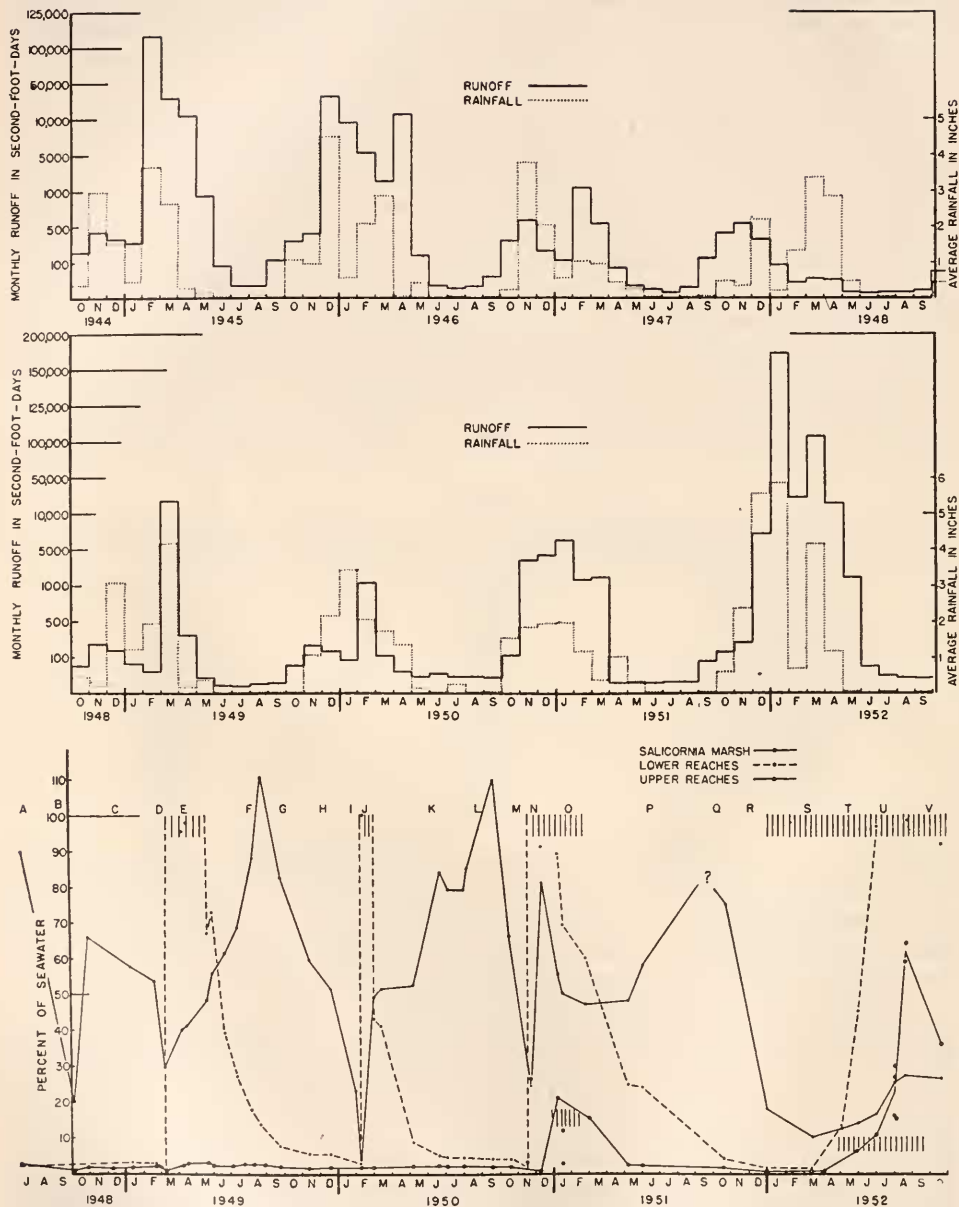


FIGURE 2. Upper and middle charts: monthly rainfall on Salinas River watershed and discharge into estuary at Spreckels, 1944-52 (note compression of runoff scale). Lower chart: salinity changes at Locations 3 (*Salicornia* marsh), 4 (upper reaches), and 1 (lower reaches), 1948-52. Letters above curves refer to points discussed in text.

PATTERN OF ANNUAL SALINITY VARIATION

It is apparent that an estuary such as that of the Salinas, in a region of variable rainfall, subject to summer diversion for irrigation and to winter floods, offers a most unstable environment, and one which can be described only in rather general terms. The observations reported below are admittedly rather superficial. The salinities are for simplicity expressed as "per cent of sea water" (taken as having a chlorinity of 19.64%, or a salinity of 35.48%). Obviously, calcium and other salts present in the distinctly "hard" Salinas River water render the river somewhat less unsuitable than its low chlorinity might suggest. This has been shown experimentally, but for purposes of giving the general pattern of variation in the brackish estuary, only chlorinity determinations have been used. Observations have usually been made at intervals of some weeks, since the Salinas lies about 100 miles from Berkeley, and were incidental to other work. Nevertheless, even scattered observations over a four-year period may contribute to an understanding of the range of variation in salinity experienced by *Neanthes lighti* in different typical habitats, and furnish a basis for appreciating the development of osmotic tolerance in a marine invader of brackish waters.

It should be noted that in the two dry winters prior to the start of this study, rainfall had been insufficient to cause the river to break through to the sea, and in the summer of 1948 the estuary was, accordingly, a quiet pond-like area of low salinity, a situation which became increasingly less stable during the following four years. Salinity determinations have been made regularly at four stations (Locations 1 to 4), and additional observations at certain others. The first three of the following stations lie in or adjacent to the lower reaches of the estuary; the last four are in the upper reaches and the head of the estuary (Fig. 1).

Location 1 represents the lower reaches of the estuary proper, below the bridges, where at times of tidal influx the salinity changes may be maximal and abrupt, but where for most of an ordinary year the water is of moderately low salinity. The bottom is of firm, somewhat muddy, fine sand, in some places underlain by clay. In these lower reaches, *N. lighti* occurs rather scatteringly and does not reach large size, a possible result of the extremely great salinity fluctuations, or of predation by wading birds at times of low tide.

Location 2 is a pool some 25 yards from the normal brink of the river, confluent with it at times of high water, but usually isolated during the summer months. *Neanthes* occurs abundantly in firm sand with an admixture of clay, black with organic matter. The salinity of the pool is variable, but is usually high, especially in summer.

Location 3 is a muddy channel winding through the *Salicornia* marsh to the south of Location 2, from which it is separated by a low roadway. This channel is isolated from the estuary except at times of flood, or at occasional high spring tides when the river mouth is open to the sea. The salinity is usually over 50% that of sea water, and may rise much higher in summer, when the channel dries up to a series of tepid pools. The bottom is of soft sandy mud, with areas of clay, quite black and foul. *N. lighti* is abundant in such areas as do not dry up entirely in summer, commonly reaching a length of 60–65 mm. preserved (Hartman, 1938, reports 45 mm. as the maximum length). The worms occupy Y-shaped burrows extending 5–8 inches into the black mud, where presumably the salinity fluctuates

far less than in the overlying water, but they are by no means insulated from this water, since the light-colored oxidized sand of the burrow walls indicates that respiratory irrigation is maintained in these passages.

The middle reaches of the estuary may be said to extend to two miles above the bridges (Fig. 1), at which point salinity variations due to tides are distinct but not extreme. At the bridges ($1\frac{3}{4}$ miles from the mouth) observations made on a single day showed that salinities varied from 3.7 to 40.4% sea water over the tidal cycle. Because of the sparse population of *Neanthes* in this area, regular salinity records were not kept. Above the bridges, the estuary is narrowed and winding. Cat-tails, tulles, and willows replace the *Salicornia* and sedges of the lower reaches. By three miles from the mouth, the estuary has taken on a superficially almost fresh water aspect. Whereas the lower reaches in dry years contain *Enteromorpha*, *Ulva*, and encrusting green algae, the upper reaches, 4-5 miles from the mouth, contain masses of *Chara* and duckweed (*Lemna*). *Potamogeton* is abundant in both areas. Four locations in the upper reaches and the head of the estuary were studied, but at only the first of these (Location 4) were regular salinity records obtained.

Location 4 represents a widened portion of river bed with sandy bars on which *N. lighti* was extremely abundant following the dry winters of 1946-7 and 1947-8, when the area was undisturbed by flood waters and the salinity varied little. At this location, in 1948, as many as 40 adult worms could be picked from a single shovelful of sand. At times of high water, it might be difficult to obtain many individuals, while floods in the winters of 1949 and following years have swept out much of this formerly productive area. Salinities at Location 4 have remained below 3% of sea water except that as the river flow slackens in the spring occasional tidal influxes have been observed to raise the salinity temporarily to 20% of sea water or more. Conditions following the outflow of early 1952 have entirely altered this and the following upstream locations; these descriptions apply to the period of relative stability prior to 1952.

Location 5 lay about one-half mile upstream from Location 4, and represented the limit of *N. lighti*, where small numbers of reproducing worms were collected in July, 1949 (chlorinity 2.2% of sea water). This collecting spot was washed out by flood waters early in 1950.

Location 6 is about a half mile above Location 5. The intervening stretch of river was lined by cat-tails and was so narrow that in spots a skiff could be poled through only with difficulty. A current was generally perceptible in all but the driest weather, hence this region could have been considered the "head" of the estuary. Chlorinities up to 1.76% of sea water have been recorded from Location 6, which represented a sandy area just below the outfall of a drainage ditch. Although topographic maps (compiled in 1947) show the limit of permanent water in the vicinity of Location 5, I have regularly been able to take a skiff another mile upstream, there being a channel several feet deep, much narrowed by encroaching rushes and floating weeds. No *Neanthes* have ever been found at Location 6, although the substrate seems entirely suitable. However, this area is separated from Location 5 by a very muddy stretch which may have acted as a barrier to migration.

Location 7 lay at what was the limit of boat passage prior to 1952, almost a

half mile from Location 6, a little over 1.5 miles above Location 4. A slight current was usually perceptible. Chlorinities up to 1.4% of sea water have been obtained in summer. No *Neanthes* have been found, and the aspect was that of a fresh-water environment. Above this point the river channel consisted of a series of pools, separated by impenetrable beds of cat-tails.

Flood waters in the winter of 1952 swept out the masses of vegetation above Location 7, widening and deepening the channel, and permitting a boat to be taken upstream for at least another mile even at low water. Locations 5 and 7 are no longer recognizable, some bars having been swept away, others covered with many feet of sand.

The above account of conditions prevailing in the summer months at seven Locations may be amplified by presenting salinity fluctuations at three of these: Location 3, representing an area of variable but high salinity; Location 4, an area of uniformly low salinity (oligohaline); and Location 1 in the lower estuary, the area subjected to the greatest salinity changes. The data on these three representative locations have been plotted in Figure 2 (bottom) where they may be compared with each other and with rainfall and runoff at corresponding times. It is apparent that a degree of regularity in the annual pattern of salinity variation existed at each location prior to the flood year 1951-52, and that in the latter water-year conditions were profoundly altered.

At the start of field observations in 1948 (Fig. 2, A) the lower reaches (Loc. 1) were almost as fresh as the upper reaches (Loc. 4), but the isolated channel in the *Salicornia* marsh (Loc. 3) to the south of the river had a salinity of 90% of sea water, and Location 2 (not plotted) was intermediate. Early fall rains (B) in 1948 temporarily dropped the salinity at Location 3 to 20% of sea water, a loss soon largely made up by seepage and mixing. The winter rains (C) of 1948-49 produced a general lowering of salinity, culminating in early March in an inundation of the *Salicornia* marsh by nearly fresh water, followed by a break-through of the river to the sea (D). This was followed by tidal influxes (E) which caused the lower reaches (Loc. 1) to alternate between fresh and salt water, while the pool near the river (Loc. 2) became filled with sea water. With the cessation of heavy rains the flow in the river dropped to a point which permitted the reestablishment of the bar across the mouth early in May. Although occasional high tides spilled across this bar, the lower river continued to freshen until the winter of 1950 (F, G). The pool at Location 2 remained cut off from the river throughout the summer of 1949 and retained a moderate salinity despite its proximity to the brackish river until the fall rains diluted it and eventually put it into shallow communication with the river in November 1949. The more remote pools of Location 3 became steadily concentrated by evaporation throughout the summer (F), reaching a salinity of 110% that of sea water, and then were diluted by fall rains (G).

Special interest attaches to the salinity at Location 4 during the period in 1949 when the lower estuary was subjected to tidal exchange. With the opening of the bar, the water level at Location 4 dropped until many *Neanthes* burrows were completely out of water, the surface of the sand becoming dry and sun-baked. Although the worms burrowed deeply to some 18 inches, a gradual depopulation of such exposed bars occurred; whether by lateral burrowing to lower areas or by dying off could not be determined. With each tide, but lagging by several hours,

the water level at Location 4 rose and fell about a foot. That this did not represent an influx of ocean water, but merely a backing-up and draining of fresh water, was established by repeated salinity determinations showing no difference between high and low water. In that year the bar closed in May, before the river flow became minimal. During the summer of 1949, Location 4 showed a slow rise in salinity to nearly 3% of sea water, with a gradual reduction after the fall rains (H). The winter rains of early 1950 resulted in the marshes along the lower river becoming flooded with nearly fresh water before the opening of the bar on February 8 (I). High tides coming during the succeeding period of lessened rainfall flooded the marshes with ocean water (J), raising the salinity at Location 3 to approximately 50% of sea water, but there was no indication of any salinity rise at Location 4. After closure of the bar at the beginning of March (1950), the river remained so high as to be confluent with the pool at Location 2, and both of these locations continued to freshen throughout the spring of 1950 (K). The hot late summer raised the salinity at Location 3 to 109.5% of sea water (L), but that at Location 2 remained low, without in any way seeming to harm the *Neanthes* present at either station, although reproduction seemed to be prevented by water temperatures near 30° C. on sunny days.

The fall of 1950 was marked by excessively heavy rains (M), which inundated Location 3 with nearly fresh water before the bar was opened on November 17. During December, high tides flooded the lower marshes with salt water (N), and as the river current slackened, eventually sent surges of sea water several miles upstream (O), where at Location 4 a salinity 21% that of sea water was recorded on January 6, 1951. Although by January 15 the chlorinity of the river water at this point had dropped to 2.4% of sea water, a value of 11.7% of sea water was obtained from water seeping into a hole in the sandbar from which worms were dug. The river mouth had practically closed by February 21, trapping within the lower estuary approximately 60% sea water, suggesting a considerable degree of mixing. By May, 1951, salinities at Location 4 had dropped to the usual 2.2% of sea water (P). A considerable salinity rise at Location 4, the result of spring tides at a period of slackening river flow, has been observed in two separate periods in four years, hence it very probably occurs in other years, and would seem to account for the higher "residual" chlorinities commonly encountered in water obtained from holes dug in the banks of the upper estuary. This may be an important factor in permitting *Neanthes* to survive beneath nearly fresh water.

The summer of 1951 was exceptionally cool and cloudy (Q). Salinity records were unavoidably interrupted, but the river remained high, confluent with the pool at Location 2, while the water in channels back from the river (Location 3) apparently did not become as concentrated by evaporation as in typical summers. Heavy December rains (R) flooded the lower marshes, and the river broke through the bar on December 30, 1951. A visit to Location 4 on January 1, 1952 showed a swirling muddy torrent pouring to the sea. Such sand bars as could be approached were found to be shifting masses of quicksand, indicating a heavy loss of *Neanthes* from this area. The great fresh water discharge during early 1952 signaled the end of the previous ecological distinctness of Locations 3 and 4. The flow into the lower reaches was high enough to inundate the *Salicornia* marshes with water of low salinity (S)—at least there is no evidence of the flooding of the marsh with sea water from a high tide at a time of slackening river flow as had

been the case in previous springs, although the Location 2 pool did receive tidal influxes. The result was that Location 3 remained at a very low salinity, and did not in the entire summer of 1952 attain a salinity in excess of 27% sea water (S, T). Concomitantly *Neanthes* virtually disappeared from Location 3; only a few very small worms were found by careful search in July. However, Location 2, which had received influxes of sea water, retained the usual pattern of high spring and summer salinity (reaching 135% of sea water on July 30), and continued to support a normal population of *Neanthes*. It is difficult to avoid the impression that the worms of Location 3 suffered heavy mortality as a result of several months of salinities below 20% of sea water.

In the case of Location 4, the destruction of the worm population was nearly complete (only a single worm rewarded several hours of intensive search on July 31, 1952). But here the loss may be more attributable to the extensive erosion, widening, and deepening of the channel at Location 4 by several months of high stream flow than to adverse effects of salinity change. With the slackening of river flow in the spring of 1952 (T), and continuing through the summer (U), tidal effects became regular in the opened river channel. The mouth of the river remained open throughout the summer of 1952, apparently as a result of tidal scouring, for the flow was not much in excess of normal. Possibly wave action in the summer months is insufficient to throw up the barrier bar if a high discharge by the river in the spring has prevented formation of the bar at the usual time. As a result, the salinity at Location 4 rose and fell more or less regularly, a range of 15 to 30% sea water being noted in the course of a single moderate tide; probably the larger tides had considerably greater effects.

The fact that some worms evidently survived the summer of 1952 in both Locations 3 and 4, and survived in normal abundance at Location 2, suggests that in future years of low rainfall we may again see conditions stabilized and new populations of *Neanthes* developed as before. The evolutionary interest pertaining to such massive depopulations followed by repopulation from a few survivors is obvious, and a re-study of physiological adaptations in the new populations, if such arise, should be made to extend the preliminary studies carried out upon the past populations.

FAUNAL ASSOCIATES OF *NEANTHES LIGHTI*

In the summers of 1949 and 1950, before the stabilized "dry-year" pattern of the Salinas estuary had been upset, collections of the fauna at the several stations were made. Although conditions have in some instances been altered drastically, the following notes give a picture of the estuarine fauna in a condition as near equilibrium as is likely to be found. Since the range of *N. lighti* shows such marked variation in salinity, and includes areas with a distinctly fresh water aspect, a tabulation of the animals associated at a given location may be of value in estimating the relative extent of the penetration of this worm into "fresh" water. The statement of Hartman (1938) that *N. lighti* may occur in freshwater pools, as judged by the associated fauna of insects, etc., should be checked by a study of actual salinities. As is shown below, the faunal associates of *N. lighti* in the Salinas River include both fresh water and brackish water types.

Location 1: Most common were the isopod *Neosphaeroma oregonensis*, and the

amphipods *Corophium spinicorne* and *Anisogammarus confervicolus*. The chief planktonic crustacean was *Neomysis mercedi*, while insects were represented by corixids and dipteran larvae. The openness of the area and the abundance of waders and sea-birds may contribute to a general paucity of fauna.

Locations 2 and 3: These contain in general the same fauna as Location 1 except the *Neomysis* is absent from both and *Corophium spinicorne* scarce at Location 3, especially at periods of high salinity. The small snail *Amnicola* occurs in large numbers on *Potamogeton* and other plants at Location 2.

Location 4: At this and the following points, collections were made from among cat-tails as well as from the adjoining sand, so that the habitats examined in the upper reaches are comparable. The fauna included the following typically fresh-water forms: *Physa*, *Chironomus*, *Plumatella*, *Hyaella asteca*, dragon-fly larvae, several dipteran larvae, bellostomid and corixid bugs, and beetle larvae. In addition, the following forms of marine affinities were well represented: *Corophium spinicorne*, *Anisogammarus confervicolus*, *Neosphaeroma oregonensis*, and *Neomysis mercedi*. Careful search revealed no planarians but a few leeches (*Placobdella fusca*).

Location 5: A small coarse sand beach contained small numbers of breeding *Neanthes* in July, 1949 (salinity 2.2% sea water). Collections in this area included essentially all the fresh water types encountered at Location 4, plus the snail *Gyraulus*, ephemeropterid and damselfly larvae and a few small planarians. *Corophium spinicorne* and *Neosphaeroma* were present but scarce. *Anisogammarus* was absent.

Location 6: Below the point where fresh water drainage ditch empties into the river, a sand bar suitable for *Neanthes* was examined, but found to harbor only chironomids and *Corophium stimpsoni*, the latter breeding and present in large numbers. Since the bottom appeared suitable and the chlorinity possibly adequate (1.75% of sea water), the absence of *Neanthes* may have been due to the long stretch of river above Location 5 which lacked suitable bottom for these worms. The fauna also differed from that at Location 5 in the absence of *Neosphaeroma* and of *Corophium spinicorne*. The replacement of the latter by *C. stimpsoni* is of especial interest. Shoemaker (1949) states that *C. spinicorne* is the only *Corophium* recorded from the fresh waters of America, but the presence of *C. stimpsoni* in the freshest part of the Salinas estuary suggests that the later species is actually more tolerant of fresh water than is *C. spinicorne*.

Location 7 was at the limit of boat passage, approximately $\frac{1}{2}$ mile from Location 6 (2 miles from Location 4). The fresh water fauna previously encountered were here in abundance, including numerous leeches and very abundant large planarians (*Dugesia* sp.). The only representative of the "marine" fauna was *Neomysis*, present in great numbers. Chlorinity was 1.4% that of sea water. The bottom was muddy and no *Corophium* were taken.

This cursory account suffices to show that the range of *Neanthes lighti* coincides in a general way with those of *Neosphaeroma oregonensis*, *Anisogammarus confervicolus*, and *Corophium spinicorne*, all of which are characteristic brackish water species. Conversely, it appears that *N. lighti* occupies a region which overlaps only slightly the ranges of such fresh water forms as planarians or leeches, although numerous fresh water insects, as well as the snail *Physa*, extend into the

less saline portions of the range of *Neanthes*. It would appear on the basis of these scanty collections that *Corophium stimpsoni* may be restricted to waters less saline than those tolerated by *Neanthes lighti*, but final judgment on this point should await a detailed study of the distribution of the several species of *Corophium* within brackish waters. Certain forms, such as *Neomysis mercedi* and the groups of the corixids and chironomids, have a much wider salinity tolerance than *N. lighti*, and are not so useful as indicators in this situation.

DISCUSSION

While Figure 2 upon first inspection seems to reveal a situation little short of chaotic, the observations over the past several years permit certain generalizations concerning the conditions of life in a small California estuary. There are, most strikingly, wide and irregular salinity variations in the lower reaches, these being most marked in the lower river channel itself, where long periods of quiet water of low salinity are interspersed with weeks or months of tidal action which may result in a daily salinity shift from 3% to 100% of sea water, as well as exposure to air and to predators. It is perhaps significant that in this area of most extreme change and exposure hazard, *Neanthes lighti* is least abundant.

These worms have been more consistently abundant, larger, and more vigorous in two general situations, differing in opposite senses from the lower estuary proper. The following remarks apply to conditions prior to the upset of 1951-52, which is considered to have been a decidedly abnormal season. At Location 3 there has usually been a salinity range of 30-40% to above 100% that of sea water. Owing to the tendency of fresh water to layer out above salt water, and for substrata of high salinity to be little affected by submergence beneath fresh water for relatively short periods (Reid, 1930, 1932), it does not seem likely that worms in their burrows in the muddy channel at Location 3 are ever abruptly exposed to salinities as low as are measured in the river itself at times of flood, or at most for very limited periods. Worms from this area can be adapted to chlorinities equivalent to 1% of sea water; hence salinity variations at Location 3 are not extremely severe. Temperatures of 30° C. in summer seem not to injure the adult worms, but result in failure of fertilization and/or development of embryos (Smith, 1950).

In marked contrast has been the prevailing low salinity at Location 4 in normal years. Over most of the period of observation, chlorinities have varied from about 3% of sea water down to as low as 0.25% at times of flood. Worms in their burrows perhaps receive protection against the lower salinities of the flowing water above them as a result of "residual" salinity in the sand of the banks and bottom. It has commonly been noted that worms collected at times of flood become much swollen if retained in river water, but survive better if kept in the sand from which they were dug. Such worms tend to form distinct "jackets" of mucus and sand, which may offer some protection. It has also been found best to keep worms collected from brackish water at room temperature, since refrigeration apparently retards active osmoregulation to such a degree that swelling and death may occur. Mixing from the lower reaches and occasional tidal influxes of sea water probably serve to maintain the slight salinity required for survival in such nearly fresh-water areas in normal years.

It is apparent that *N. lighti* is a brackish-water type which has not completed the

transition to a strictly fresh water habitat. From a study of conditions in the Salinas River it is not possible to say whether this transition could be made. From the fact that the range of *N. lighti* seems to coincide with that of such forms as *Corophium spinicorne* and *Neosphaeroma oregonensis*, but does not extend so far upstream as that of *Corophium stimpsoni* or *Neomysis mercedi*, we may judge that it is actually limited in its osmoregulatory abilities. Furthermore, the dropping out of such typically fresh water forms as odonata larvae, planarians, and leeches as the fresh water fauna approaches the upper limit of *N. lighti* suggests that the salinities required by *N. lighti* are not inappreciable, inasmuch as they may limit the seaward extension of these fresh water animals.

Physical barriers to the upstream spread of *N. lighti* appear serious, but are difficult to evaluate precisely. Recurrent rushes of flood water have been observed to sweep away well-populated sand bars, or to cover productive areas with thick layers of barren sand. Thus the bar at Location 5, which in 1949 marked the upstream limit of *N. lighti*, was completely washed away in February, 1950, and the area has not been repopulated. Another factor which may have limited the spread upstream beyond Location 5 is the fact that the stream above this point became thickly bordered by cat-tails growing in very soft black mud. *N. lighti* seems to require a sandy substrate for its burrows, and has never been taken in the sort of mud found for the half mile above Location 5. There is usually a perceptible current in this area, even in summer in dry years, which may have further discouraged upstream migration of young worms.

The nereid population of the upper reaches has been in several senses isolated from that of the *Salicornia* marshes: First, by the fact that the normal range of salinities at Location 4 does not (except for infrequent and brief periods) overlap the range of salinities at Location 3. Second, by the presence of intervening stretches of river physically poorly suited for large populations of *Neanthes*. Third, by the fact that *N. lighti* appears to consist of self-fertilizing hermaphroditic viviparous individuals, which do not produce widely-dispersing planktonic larvae. The problem of whether or not these populations constitute actual physiological races requires more detailed study. Preliminary studies have been made to ascertain this point, but since the studies cannot be confirmed until conditions in the estuary have become stabilized and new populations developed, only an abstract of these studies need be included here. In this work, the respiration of worms from Location 4 was compared with that of worms from Location 3. The method used was to adapt worms from each area gradually to a series of different salinities (1, 5, 10, 50, 100, and over 100% of sea water), and to maintain them (with feeding) at these salinities for three or more weeks to ensure full adaptation. It was considered that the worms became nearly as fully adapted to the test salinities as their physiological constitutions would permit. It was found that worms from Location 3, adapted to salinities 5% or less of sea water showed a higher respiration on the average than did worms from Location 4 adapted to identical media. Since a number of variables, including size, had to be taken into account, the results, although apparently significant, are considered indicative of, rather than conclusive evidence for, the existence of physiologically distinct races of *N. lighti* in different parts of the Salinas estuary. The drastic reduction of the populations in question following the hydrographic upset of 1951-52 further suggests that these populations were physiologically specialized or distinct. Because the upset of

stable conditions will delay completion of these studies for some time, until the estuary stabilizes, the work will not be reported in detail until it can be confirmed.

SUMMARY

1. Salinity and salinity changes have been studied over the range of the polychaete *Neanthes lighti* Hartman in the estuary of the Salinas River, California, during the years 1948-1952.

2. Not only are mean salinities different in various parts of the range of *N. lighti*, but each locality has a characteristic annual pattern of salinity variation depending upon fresh water discharge into the estuary.

3. The pattern of salinity variation is traced through years of low and moderate rainfall, and its upset during the flood season of 1951-52 is reported.

4. Worms inhabiting marshy areas near the river mouth are exposed to variable but high salinities (40 to over 100% of sea water); those in the upper reaches endure uniformly oligohaline conditions (2-3% of sea water) for most of the year. Either of these areas is more favorable than the lower reaches of the estuary that receive full tidal exchanges for part of each year.

5. Over its range, *N. lighti* is associated with such typically brackish water species as *Ncosphaeroma oregonensis* (Dana), *Anisogammarus confervicolus* (Stimpson), and *Corophium spinicorne* Stimpson. Its range only slightly overlaps the ranges of such fresh water forms as *Dugesia* sp., leeches, or odonata larvae. *Corophium stimpsoni* Shoemaker is found in water fresher than that inhabited by *N. lighti* or the crustaceans associated with it.

6. The populations of *N. lighti* of the upper reaches are ecologically and reproductively isolated from those of the more saline marsh channels, and some evidence for the existence of physiological distinctness between these populations has been found.

LITERATURE CITED

- DAY, J. H., 1951. The ecology of South African estuaries. Part I. A review of estuarine conditions in general. *Trans. Roy. Soc. South Africa*, **33**: 53-91.
- HARTMAN, O., 1938. Brackish and fresh-water Nereidae from the northeast Pacific, with the description of a new species from central California. *Univ. Calif. Publ. Zool.*, **43**: 79-82.
- MACGINITIE, G. E., 1935. Ecological aspects of a California marine estuary. *Amer. Midl. Nat.*, **16**: 629-765.
- REID, D. M., 1930. Salinity interchange between seawater in sand and overflowing fresh-water at low tide. *J. Mar. Biol. Assoc.*, **16**: 609-614.
- REID, D. M., 1932. Salinity interchange between salt water in sand and overflowing fresh-water at low tide. *J. Mar. Biol. Assoc.*, **18**: 299-306.
- SCOTT, K. M. F., A. D. HARRISON AND W. MACNAE, 1952. The ecology of South African Estuaries. Part II. The Klein River Estuary, Hermanus, Cape. *Trans. Roy. Soc. South Africa*, **33**: 283-331, pl. 25-26.
- SHOEMAKER, C. R., 1949. The amphipod genus *Corophium* on the west coast of America. *J. Wash. Acad. Sci.*, **39**: 66-82.
- SMITH, R. I., 1950. Embryonic development in the viviparous nereid polychaete, *Neanthes lighti* Hartman. *J. Morph.*, **87**: 417-465.
- U. S. Department of Commerce Weather Bureau. "Climatological Data, California Section." 1944-1952.
- U. S. Department of the Interior, Geological Survey Water Supply Papers, "Surface Water Supply of the United States," Part 11, Pacific Slope Basins in California, 1944-1952.